

RESEARCH PAPER

Generation mean analysis of quantitative traits in restorer lines of rice (*Oryza sativa* L.)

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Gene action and inheritance of quantitative traits associated with good out-pollination, agronomic and grain quality in restorer lines of rice was studied by generation mean analysis through six parameter model of Hayman. Eleven traits namely days to 50 per cent flowering, flag leaf area, plant height, number of panicles plant⁻¹, panicle length, number of filled grains panicle⁻¹, 100 seed weight, grain yield plant⁻¹, kernel length, kernel breadth and kernel length/breadth ratio were studied in five crosses viz., BCW 56 / C20 R, BCW 56 / 1005, C 20 R / DR 714-1-2R, C 20 R / 1005 and DR 714-1-2R / 1005. The A, B, C and D scales are significant and epistasis was noticed for all the characters in all the crosses except for plant height in cross BCW56/C20R, 100 seed weight in C20 R/DR 714-1-2R and kernel breadth in C 20 R / 1005. Grain yield plant⁻¹ recorded dominance variance in all the crosses. Hence, heterosis breeding can be exploited in all the crosses by crossing the parents with high yielding CMS sources for identifying heterotic combinations. Additive and non additive gene effects with duplicate type of epistasis was observed for yield and quality characters like plant height, number of panicles plant⁻¹, panicle length, number of filled grains panicle⁻¹, 100 seed weight, grain yield plant⁻¹, kernel length, kernel breadth and kernel L/B ratio in most of the crosses studied. Biparental mating, reciprocal recurrent selection and diallele selective mating systems could be exploited to obtain desirable recombinants having the characteristics of a restorer line with tallness, desirable flowering duration, reduced flag leaf area and more number of fertile spikelets. In crosses BCW 56 / C 20 R and BCW 56 / 1005 biparental mating followed by selection will be desirable to utilize both additive and non-additive gene action for number of filled grains panicle⁻¹ and grain yield plant⁻¹. The fixable gene effects namely additive (*d*) and additive x additive (*i*) gene effects were highly significant for the traits days to 50 per cent flowering in BCW 56 x C 20 R and C 20 R / DR 714-1-2R and 100 seed weight in crosses BCW 56 / C 20 R and C 20 R / 1005 and offer scope for improvement through phenotypic selection based on pedigree method in segregating generations by isolating desirable lines for the important floral, yield and quality traits for use as male parents in hybridization programmes.

Key words : Gene action, Quantitative traits, Generation mean analysis, Restorer lines, Rice

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INTRODUCTION

Rice is a premium food grain crop and is often the

main source of calories and principal food of millions of people. Though the green revolution has helped to attain

self-sufficiency in food grain production, in coming decades the production needs to be increased every year by almost two million tones to meet the growing needs of increasing population. Moreover, with changing consumer preferences and the demand by the export market, improvement in grain quality has to convene with yield. Under the present context of shrinking natural resources, climate change and burgeoning population, the only choice is to increase the productivity by enhancing the yield levels. Among the many genetic approaches being exploited to increase the yield levels, hybrid rice technology using three line system appears to be the most appropriate, ecofriendly and readily adoptable one. However, the extent of adoption of hybrid rice technology to increase the paddy production has been much slower than the expected due to several reasons like marginal and inconsistent yield advantages, unacceptable grain quality, inadequate profitability by cultivation of hybrids at present market prices and higher seed cost due to seed production difficulties. To increase the economic advantage of this technology and for ready acceptance by the farmers on a large scale, hybrid rice technology has to be improved further. This needs concerted research efforts in certain areas like identification and development of location specific diverse parental lines (maintainers and restorers), to study heterosis for yield, development of heterotic hybrids, efficient and economic hybrid seed production techniques and effective technology transfer efforts.

Most commercial indica hybrid rices have been developed through the wild abortive (WA) cytoplasmic male sterility (CMS) system, maintainer (B) and restorer (R) lines. The fertility of WA type CMS line, the most widely used source, is generally restored by various IR varieties and strains (Virmani, 1986) with 20-30 per cent heterosis for grain yield (Huang *et al.*, 1984). Effective and diverse restorer lines are necessary to exploit heterosis. The higher the genetic variability, the greater is the probability of obtaining heterotic combinations since, heterosis is directly proportional to Σdy^2 where 'd' is the degree of dominance component of gene action and 'y' is the difference in the gene frequencies of the parents involved in the cross (Falconer, 1960).

Desirable restorer lines should possess good fertility restoration ability, high performance for yield and yield contributing characters, multiple disease and pest resistance, good general combining ability, high pollen

production with high residual pollen and dispersal ability, and good grain quality traits. Several elite IR lines possessing good combining ability and strong heterosis were being discarded due to their weak restoring ability and other floral traits associated with out-pollination. Since, effective and diverse restorer lines and CMS lines are necessary to exploit heterosis, improvement programmes were designed to develop simultaneously both the CMS lines and restorer lines. The concept of location specific CMS lines to suit different agro-climatic conditions was emerged to face problems like genetic uniformity and genetic vulnerability. Identification of genetically diverse restorer lines and developing heterogenous gene pool of restorers for these locally adaptable new CMS lines is the need of the hour and can be achieved through cross breeding (Restorer x Restorer) and genetic male sterility facilitated recurrent selection programmes (DRR, 2005). Cross breeding (Restorer x Restorer) is adopted for development of allo-cytoplasmic restorers (restorer lines which have normal cytoplasm are called allo-cytoplasmic restorers) with increased magnitude of heterosis through broadening the genetic base (DRR, 2005).

The choice of an efficient breeding program depends to a large extent on the knowledge of the type of gene action involved in the expression of the characters being improved. Application of biometrical procedures like generation mean analysis helps in providing information about the type of inter-allelic interaction and genetic components of variance underlying genetics of quantitative characters. This helps the plant breeder to systematically analyze the inheritance patterns and plan for result oriented breeding programmes. Many reports are available on the nature of gene action governing yield and its component traits in rice. Partitioning of gene effects through generation mean analysis has not been adequately tested for genetic improvement of restorer lines in rice. Studies on the gene action and inheritance of traits associated with flowering and yield traits of restorer lines are very limited. Keeping in view the need to develop improved restorer lines for utilization in enhancing the magnitude of heterosis of rice hybrids, an attempt was made in the present study to unravel the genetic architecture of some of the important floral, agronomic and grain quality traits in restorer lines of rice.

RESEARCH METHODOLOGY

The present study was conducted using eight

restorer lines namely, C 20 R (collected from Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India), KMR 3 (from University of Agricultural Sciences, Mandya, Karnataka, India), BCW 56, DR 714-1-2R, EPLT 104, SC₅-9-3, 619-2 and 1005 from Directorate of Rice Research, Hyderabad, Andhra Pradesh, India) crossed in a half diallel mating design to obtain 28 F₁ hybrids during *Rabi*, 2006 in a crossing block at Directorate of Rice Research, Hyderabad, Andhra Pradesh. In *Kharif* 2007, F₁ hybrids were evaluated and selected five crosses viz., BCW 56 / C20 R, BCW 56 / 1005, C 20 R / DR 714-1-2R, C 20 R / 1005 and DR 714-1-2R / 1005 based on their high *per se* performance and *gca* effects for floral traits (days to 50% flowering, duration of blooming and residual pollen per anther), grain yield and quality characters and diversity among parents for studying gene effects through generation mean analysis. All the six generations in each of the five crosses were generated during *Kharif* and *Rabi*, 2007.

In *Kharif* 2008, the material of six basic generations was raised in a Randomized Block Design with three replications. A row length of 4 m length with spacing of 20 x 15 cm for parents and 20 x 20 cm for F₁, F₂, B₁ and B₂ generations was followed. The F₂ seed from each individually threshed F₁ plant was planted in rows and a total of twenty rows (400 seedlings/replication) were maintained for F₂ generation of each cross. The backcrosses were sown in twelve rows (240 seedlings/replication), whereas parents and hybrids were planted in three rows (60 seedlings/replication). Single seedling was planted per hill and the recommended package of practices and prophylactic measures were followed to raise a healthy crop. Data were recorded on randomly selected 10 plants from each of the parents (P₁ and P₂) and F₁, 90 plants in F₂ and 60 plants each in B₁ and B₂ generations.

Eleven traits including days to 50 per cent flowering (was recorded on individual plants in F₂ and backcross generations as the total numbers of days taken for 50 % of the panicle to flower from the date of sowing and on plot basis in other generations), flag leaf area (cm²), plant height (cm), number of panicles plant⁻¹, panicle length (cm), number of filled grains panicle⁻¹, 100-seed weight (g), grain yield plant⁻¹(g), kernel length (mm), kernel breadth (mm) and kernel length/breadth ratio were recorded as per standard evaluation system (SES) of rice (IRRI, 2002).

Data analysis :

Generation mean analysis (GMA) developed by Hayman (1958) was utilized to estimate the genetic components of variation. Scaling test was conducted for testing the presence / absence of gene interaction. The adequacy of additive-dominance model was tested by calculating different scales followed by variances and standard errors as suggested by Mather (1949) and Hayman and Mather (1955). The significance of any one of the scaling tests indicated the presence of epistasis. When the model was adequate (when the scales were significant), the mean values over replications are used for the estimation of the gene effects by six parameter model proposed by Hayman (1958) viz., mean (*m*), additive gene effects (*d*), dominance gene effects (*h*) and three types of non-allelic gene interactions viz., additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*). Variance and standard error of each estimates was calculated to test the significance of the calculated gene effects by 't' test.

RESEARCH FINDINGS AND ANALYSIS

The analyses of variance for the five crosses for eleven characters (floral, yield and grain quality traits) are presented in Table 1. The analysis of variance revealed significant differences among the generations for various characters in all the five crosses except for kernel L/B ratio in cross BCW 56 / 1005 and plant height in cross C 20 R / 1005. Since the differences between different generation means were found to be non-significant for these two characters, further analysis of these characters (*i.e.*, kernel L/B ratio in cross BCW 56 / 1005 and plant height in cross C 20 R / 1005) was avoided and generation means of the remaining crosses are subjected to generation mean analysis to know the gene action controlling the traits.

Results of the individual scaling tests (Table 2) were non-significant for plant height in BCW 56/C20R, 100 seed weight in C 20 R/DR 714-1-2R and kernel breadth in C 20 R / 1005 indicating the absence of epistasis-interaction for these traits in the respective crosses. Thus, the characters plant height, 100 seed weight and kernel breadth in the respective crosses showed simple type of inheritance, while epistasis contributed significantly towards the inheritance of the remaining characters in all other crosses.

The study of gene effects (Table 3) revealed that

Table 1: Analysis of variance of six generations for quantitative characters in five crosses of rice

Sr. No.	Source of variation	d.f.	Mean squares				
			Cross 1	Cross 2	Cross 3	Cross 4	Cross 5
1.	Days to 50 per cent flowering						
	Replications	2	5.37	0.55	4.96	4.87	0.25
	Generations	5	61.98**	51.47**	65.87**	198.46**	123.90**
	Error	10	1.55	2.61	3.78	4.17	0.44
2.	Flag leaf area						
	Replications	2	1.29	4.33	5.61*	2.15	3.82
	Generations	5	45.28**	74.08**	24.96**	75.99**	80.99**
	Error	10	1.57	4.91	1.25	6.89	1.89
3.	Plant height						
	Replications	2	0.76	6.55	0.79	1.13	1.60
	Generations	5	254.99**	241.21**	61.22**	4.80	85.31**
	Error	10	0.96	2.24	1.03	2.18	1.07
4.	Number of panicles per plant						
	Replications	2	0.01	0.04	0.08	0.02	0.07
	Generations	5	2.67**	7.53**	11.66**	6.76**	11.25**
	Error	10	0.05	0.09	0.08	0.11	0.10
5.	Panicle length						
	Replications	2	0.80	0.12	0.31	0.54	0.11
	Generations	5	37.10**	19.81**	13.21**	7.67**	8.22**
	Error	10	0.22	0.25	0.27	0.79	0.36
6.	Number of filled grains per panicle						
	Replications	2	5.92	21.89	12.45	53.18	7.01
	Generations	5	1534.46**	4021.93**	891.64**	825.76**	2422.69**
	Error	10	13.80	20.015	3.19	79.98	16.45
7.	100- seed weight						
	Replications	2	0.00	0.00	0.00	0.00	0.00
	Generations	5	0.00*	0.39**	0.01*	0.42**	0.25**
	Error	10	0.00	0.00	0.00	0.00	0.00
8.	Grain yield per plant						
	Replications	2	0.68	0.48	0.25	1.47	0.03
	Generations	5	32.24**	173.26**	90.50**	34.84*	21.99**
	Error	10	1.06	0.82	0.55	1.57	0.50
9.	Kernel length						
	Replications	2	0.02	0.01	0.03	0.00	0.02
	Generations	5	0.40**	0.21**	0.92**	0.15**	0.66**
	Error	10	0.02	0.03	0.01	0.01	0.01
10.	Kernel breadth						
	Replications	2	0.00	0.00	0.00	0.00	0.00
	Generations	5	0.04**	0.05**	0.08**	0.17**	0.03**
	Error	10	0.00	0.00	0.00	0.00	0.00
11.	Kernel L/B ratio						
	Replications	2	0.00	0.00	0.00	0.00	0.01
	Generations	5	0.22**	0.02	0.58**	0.34**	0.09**
	Error	10	0.01	0.01	0.00	0.01	0.01

Cross 1: BCW 56 / C20 R; Cross 2: BCW 56 / 1005; Cross 3: C 20 R / DR 714-1-2R; Cross 4: C 20 R / 1005; Cross 5: DR 714-1-2R / 1005

* and ** indicate significance of values at P=0.05 and 0.01, respectively

Table 2: Scaling tests foreleven quantitative characters in five crosses of restorer lines in rice

Cross combination	Scales			
	A	B	C	D
Days to 50% flowering				
BCW 56 / C 20 R	-0.73 ± 1.47	-1.5 ± 1.70	-15.98** ± 5.33	-6.87* ± 2.86
BCW 56 / 1005	-6.93** ± 1.85	-2.43 ± 1.26	-16.73** ± 3.05	-3.68* ± 1.74
C 20 R / DR714-1-2R	3.87** ± 1.74	3.87** ± 1.74	-2.91 ± 2.50	-4.86** ± 1.59
C 20 R / 1005	-23.83** ± 1.53	-24.17** ± 1.68	-71.69** ± 2.22	-11.84** ± 1.57
DR 714-1-2R / 1005	1.00 ± 1.42	-1.37** ± 0.41	41.31** ± 2.15	20.84** ± 1.23
Flag leaf area				
BCW 56 / C 20 R	-5.35** ± 1.05	2.52 ± 1.30	-12.83** ± 2.10	-5.00** ± 1.14
BCW 56 / 1005	-1.56 ± 1.45	-5.63** ± 1.75	-31.26** ± 3.63	-12.04** ± 1.72
C 20 R / DR714-1-2R	5.53** ± 1.23	3.20** ± 1.24	10.52** ± 2.56	0.89 ± 0.87
C 20 R / 1005	-0.19 ± 1.57	-4.66** ± 2.00	11.92** ± 4.28	8.38** ± 1.89
DR 714-1-2R / 1005	2.50* ± 1.21	-2.81 ± 1.60	-1.54 ± 2.89	-0.62 ± 1.34
Plant height				
BCW 56 / C 20 R	-2.83 ± 1.82	3.72 ± 1.98	-4.53 ± 4.21	-2.71 ± 2.33
BCW 56 / 1005	-2.57 ± 1.86	-1.03 ± 1.65	-21.71** ± 4.19	-9.06** ± 2.29
C 20 R / DR714-1-2R	3.78** ± 1.16	2.98 ± 1.76	21.74** ± 3.26	7.49** ± 1.82
C 20 R / 1005	--	--	--	--
DR 714-1-2R / 1005	5.89** ± 1.54	4.32** ± 1.33	7.30* ± 3.53	-1.45 ± 1.88
Number of panicle per plant				
BCW 56 / C 20 R	-1.47 ** ± 0.50	-0.77 ± 0.41	0.18 ± 1.24	1.21* ± 0.59
BCW 56 / 1005	-1.53** ± 0.58	-1.90** ± 0.55	-4.78** ± 1.29	-0.67 ± 0.64
C 20 R / DR 714-1-2R	-2.87** ± 0.49	-2.70** ± 0.37	-0.80 ± 1.42	2.38** ± 0.73
C 20 R / 1005	-1.60** ± 0.41	-1.50** ± 0.46	-6.24** ± 1.47	-1.57* ± 0.73
DR 714-1-2R / 1005	-4.80** ± 0.38	-2.17** ± 0.48	-14.87** ± 1.36	-3.95** ± 0.67
Panicle length				
BCW 56 / C 20 R	-2.44** ± 0.77	1.04 ± 0.79	-4.78** ± 1.22	-1.69** ± 0.66
BCW 56 / 1005	-5.50** ± 0.79	-0.15 ± 0.64	-13.06** ± 1.60	-3.70** ± 0.84
C 20 R / DR 714-1-2R	1.75 ** ± 0.74	-0.06 ± 0.55	4.98 ** ± 1.09	1.65 ** ± 0.58
C 20 R / 1005	-0.3 ± 0.64	-0.24 ± 0.70	4.40** ± 1.43	2.47** ± 0.72
DR 714-1-2R / 1005	0.24 ± 0.55	0.90* ± 0.45	11.21** ± 1.12	5.03** ± 0.55
Number of filled grains per panicle				
BCW 56 / C 20 R	-18.17** ± 3.07	-19.33** ± 3.47	-233.42** ± 9.79	-97.96** ± 4.60
BCW 56 / 1005	-56.27** ± 4.97	-29.53** ± 5.57	-350.13** ± 14.96	-132.17** ± 6.39
C 20 R / DR 714-1-2R	-5.27 ± 3.98	1.23 ± 1.85	-89.02 ** ± 7.80	-42.49 ** ± 3.68
C 20 R / 1005	-9.43** ± 3.13	-5.73* ± 2.30	67.51** ± 15.70	41.34** ± 7.73
DR 714-1-2R / 1005	1.7 ± 2.51	16.87** ± 3.38	69.64** ± 13.28	25.54** ± 6.82
100 seed weight				
BCW 56 / C 20 R	-0.10* ± 0.05	-0.02 ± 0.03	-0.18 ± 0.11	-0.03 ± 0.05
BCW 56 / 1005	-0.01 ± 0.05	0.11 ± 0.08	-0.30 ** ± 0.11	-0.20 ** ± 0.07
20 R / DR 714-1-2R	-0.02 ± 0.03	0.00 ± 0.03	-0.07 ± 0.09	-0.03 ± 0.04
C 20 R / 1005	0.06 ± 0.04	-0.20** ± 0.05	-1.01** ± 0.10	-0.44** ± 0.05
DR 714-1-2R / 1005	0.06* ± 0.03	0.09 ± 0.07	0.15 ± 0.10	0.00 ± 0.06
Kernel length				
BCW 56 / C 20 R	-0.11 ± 0.10	0.24 * ± 0.10	0.25 ± 0.22	0.06 ± 0.11
BCW 56 / 1005	-0.30** ± 0.11	0.00 ± 0.10	0.04 ± 0.23	0.17 ± 0.10

Table 2 : Contd.....

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C 20 R / DR 714-1-2R	0.10 ± 0.09	0.09 ± 0.15	-0.34 ± 0.20	-0.26** ± 0.10
C 20 R / 1005	-0.37** ± 0.06	-0.08 ± 0.07	-0.97** ± 0.15	-0.26** ± 0.06
DR 714-1-2R / 1005	0.34** ± 0.01	0.04 ± 0.01	-0.53* ± 0.05	-0.46** ± 0.01
Kernel breadth				
BCW 56 / C 20 R	-0.07 ± 0.05	-0.06 ± 0.04	0.06 ± 0.10	0.10* ± 0.04
BCW 56 / 1005	0.01 ± 0.04	0.14** ± 0.05	0.25** ± 0.10	0.05 ± 0.04
C 20 R / DR 714-1-2R	-0.05 ± 0.05	-0.03 ± 0.05	0.40** ± 0.09	0.24** ± 0.04
C 20 R / 1005	-0.01 ± 0.04	0.10 ± 0.05	0.06 ± 0.12	-0.02 ± 0.05
DR 714-1-2R / 1005	0.00 ± 0.04	0.07 ± 0.04	0.47** ± 0.10	0.20** ± 0.04
Kernel l/b ratio				
BCW 56 / C 20 R	0.02 ± 0.08	0.15* ± 0.06	0.03 ± 0.14	-0.07 ± 0.07
BCW 56 / 1005	--	--	--	--
C 20 R / DR 714-1-2R	0.07 ± 0.07	0.07 ± 0.12	-0.67** ± 0.14	-0.41** ± 0.08
C 20 R / 1005	-0.16** ± 0.04	-0.23** ± 0.08	-0.54** ± 0.15	-0.08 ± 0.06
DR 714-1-2R / 1005	0.16* ± 0.07	-0.09 ± 0.08	-0.94** ± 0.19	-0.50** ± 0.08
Grain yield per plant				
BCW 56 / C 20 R	-6.01 ** ± 1.18	-4.99 ** ± 1.10	-30.09 ** ± 2.75	-9.55 ** ± 1.26
BCW 56 / 1005	-11.78** ± 2.11	-7.75** ± 2.10	-57.22** ± 4.16	-18.84** ± 1.49
C 20 R / DR 714-1-2R	-8.13 ** ± 1.22	-6.80 ** ± 0.76	-17.45 ** ± 2.78	-1.26 ± 1.48
C 20 R / 1005	-3.97** ± 1.06	-3.78** ± 1.15	-8.63* ± 4.31	-0.44 ± 2.18
DR 714-1-2R / 1005	-6.27** ± 0.72	1.72 ± 1.14	-9.74** ± 3.07	-2.59 ± 1.55

* and ** indicate significance of values at P=0.05 and 0.01, respectively

additive (*d*) and additive x additive (*i*) gene effects were significant in the inheritance of the trait days to 50 per cent flowering in crosses BCW 56 / C 20 R (*d* = 4.35** and *i* = 13.74**), BCW 56/1005 (*i* = 7.37**) and C 20 R / DR 714 -1- 2R (*d* = 5.83** and *i* = 9.71**) indicating the predominance of fixable gene interaction controlling this trait, suggesting that simple pedigree selection in the segregating generations helps in identifying homozygous lines for flowering period, a trait that is essential for better synchronization of flowering during hybrid seed production. The crosses C 20 R / 1005 and DR 714-1-2R / 1005 were highly significant for additive x additive '*i*', dominance '*h*' and dominance x dominance '*l*' components indicating the role of both additive and non-additive gene action in controlling this trait. The breeding approaches other than simple pedigree selection which can utilize both types of gene actions help in recovering desirable types in the segregating generations. In cross, C 20 R / 1005, the '*h*' and '*l*' component is of complementary type which suggest that improvement of flowering trait can be obtained in the segregating generations. Similar results were also reported by Hasib *et al.* (2002).

All types of gene effects *i.e.*, '*d*', '*h*', '*i*', '*j*' and '*l*'

epistatic components were highly significant for flag leaf area, a very important character of restorer line in rice. As also the additive x additive and dominance played a major role in crosses BCW 56 / C 20 R and BCW 56 / 1005 for flag leaf area. Plant height, which is another important trait of restorer line, is also under additive control in two crosses *viz.*, BCW 56 / 1005 and C20 R / DR 714-1-2R. Hence, as such these crosses can be utilized to derive improved lines through selections in the early segregating generations for plant height. While the cross BCW 56 / 1005 exhibited significant gene effects for '*d*', '*h*' and '*i*', components, therefore, biparental mating and reciprocal recurrent selections which utilize both additive and non-additive gene actions can be utilized for improving this trait in this cross. All the crosses exhibited duplicate type of epistasis for flag leaf area and plant height. Similar results were also reported by Ram (1994) and Hasib *et al.* (2002).

Number of panicles per plant recorded significant '*h*' and '*i*' epistatic components in two crosses *viz.*, C 20 R / 1005 and DR 714-1-2R / 1005. Therefore, biparental mating design followed by selections is suitable for improving number of panicles per plant. The cross BCW 56 / 1005 exhibited significant non-additive gene action

Table 3: Estimation of gene effects for eleven quantitative characters in five crosses of restorer lines in rice

Table 3: Estimation of gene effects for eleven quantitative characters in five crosses of restorer lines in rice							
Cross combination	Gene effect					Type of epistasis	
	<i>m</i>	<i>d</i>	<i>h</i>	<i>i</i>	<i>j</i>		
Days to 50% flowering							
BCW 56 / C 20 R	99.06** ± 1.32	4.35** ± 1.08	5.91 ± 5.73	13.74** ± 5.80	0.38 ± 1.10	-11.51 ± 6.87	Duplicate
BCW 56 / 1005	100.00* ± 0.70	0.65 ± 1.03	-0.33 ± 3.54	7.37* ± 3.49	-2.25* ± 1.04	2.00 ± 5.14	Duplicate
C 20 R / DR714-1-2R	93.49** ± 0.58	5.83** ± 1.10	2.88 ± 3.22	9.71** ± 3.19	0.47 ± 1.13	-16.51 ± 5.06	Duplicate
C 20 R / 1005	85.41** ± 0.55	-0.9 ± 1.13	22.22** ± 3.15	23.69** ± 3.15	0.17 ± 1.13	24.31** ± 5.02	Complementary
DR 714-1-2R / 1005	111.18** ± 0.51	-5.25** ± 0.68	-37.38** ± 2.48	-41.68** ± 2.46	1.18** ± 0.73	42.04** ± 3.47	Duplicate
Flag leaf area							
BCW 56 / C 20 R	20.28** ± 0.45	0.38 ± 0.69	9.32** ± 2.34	10.00** ± 2.27	-3.93** ± 0.79	-7.17* ± 3.47	Duplicate
BCW 56 / 1005	25.22** ± 0.77	0.95 ± 0.77	31.67** ± 3.57	24.07** ± 3.44	2.04 ± 1.04	-16.88** ± 4.76	Duplicate
C 20 R / DR714-1-2R	23.45** ± 0.38	1.48** ± 0.42	2.54 ± 2.03	-1.79 ± 1.75	1.16* ± 0.55	-6.94* ± 3.06	Duplicate
C 20 R / 1005	28.35** ± 0.86	-3.44** ± 0.77	-15.32** ± 3.99	-16.77** ± 3.78	2.23* ± 1.02	21.62** ± 5.27	Duplicate
DR 714-1-2R / 1005	25.25** ± 0.59	-3.34** ± 0.66	3.85 ± 2.81	1.23 ± 2.69	2.66** ± 0.92	-0.94 ± 3.90	Duplicate
Plant height							
BCW 56 / C 20 R	--	--	--	--	--	--	--
BCW 56 / 1005	92.12** ± 1.00	11.47** ± 1.13	14.34** ± 4.63	18.11** ± 4.58	-0.77 ± 1.18	-14.51* ± 6.17	Duplicate
C 20 R / DR714-1-2R	86.50** ± 0.77	5.48** ± 0.96	-11.62** ± 3.67	-14.99** ± 3.63	0.4 ± 1.01	8.23 ± 5.03	Duplicate
C 20 R / 1005	--	--	--	--	--	--	--
DR 714-1-2R / 1005	85.68** ± 0.83	-5.66* ± 0.88	9.12* ± 3.81	2.91 ± 3.76	0.79 ± 0.96	-13.12** ± 5.00	Duplicate
Number of panicle per plant							
BCW 56 / C 20 R	6.74** ± 0.27	-0.48* ± 0.23	0.06 ± 1.22	-2.41* ± 1.18	-0.35 ± 0.26	4.64** ± 1.54	Complementary
BCW 56 / 1005	7.06** ± 0.28	-0.78* ± 0.30	5.24** ± 1.31	1.34 ± 1.28	0.18 ± 0.36	2.09 ± 1.77	Complementary
C 20 R / DR 714-1-2R	9.13** ± 0.34	-1.82** ± 0.27	-0.77 ± 1.48	-4.77** ± 1.47	-0.08 ± 0.29	10.33** ± 1.77	Duplicate
C 20 R / 1005	6.69** ± 0.35	-0.88** ± 0.23	6.78** ± 1.49	3.14* ± 1.47	-0.05 ± 0.28	-0.04 ± 1.74	Duplicate
DR 714-1-2R / 1005	6.37** ± 0.32	-0.42 ± 0.22	11.73** ± 1.36	7.90** ± 1.34	-1.32** ± 0.27	-0.93 ± 1.62	Duplicate
Panicle length							
BCW 56 / C 20 R	20.62** ± 0.24	3.46** ± 0.45	4.57** ± 1.38	3.38* ± 1.32	-1.74** ± 0.52	-1.98 ± 2.18	Duplicate
BCW 56 / 1005	20.81** ± 0.36	0.73 ± 0.43	9.53** ± 1.72	7.41** ± 1.69	-2.68** ± 0.48	-1.76 ± 2.34	Duplicate
C 20 R / DR 714-1-2R	21.18** ± 0.22	-0.95* ± 0.38	0.83 ± 1.20	-3.29** ± 1.16	0.91* ± 0.43	1.61 ± 1.86	Complementary
C 20 R / 1005	19.99** ± 0.31	-1.82** ± 0.38	-2.79 ± 1.49	-4.94** ± 1.44	-0.03 ± 0.42	5.48** ± 2.08	Duplicate
DR 714-1-2R / 1005	23.92** ± 0.24	-0.27 ± 0.27	-7.18** ± 1.14	-10.07** ± 1.10	-0.33 ± 0.31	8.93** ± 1.57	Duplicate
Number of filled grains per panicle							
BCW 56 / C 20 R	49.34** ± 2.19	3.18* ± 1.39	200.52** ± 9.45	195.92** ± 9.19	0.58 ± 1.99	-158.42** ± 11.27	Duplicate
BCW 56 / 1005	50.37** ± 3.04	-30.37** ± 1.95	260.13** ± 13.51	264.33** ± 12.79	-13.37** ± 2.26	-178.53** ± 16.88	Duplicate

Table 3 : Contd

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C 20 R / DR 714-1-2R	76.84 ** ± 1.59	13.88** ± 1.48	111.86** ± 7.62	84.99** ± 7.37	-3.25 ± 1.90	-80.96** ± 9.78	Duplicate
C 20 R / 1005	133.41** ± 3.82	-21.45** ± 1.08	-94.41** ± 15.55	-82.68** ± 15.45	-1.35 ± 1.80	97.84** ± 16.29	Duplicate
DR 714-1-2R / 1005	114.31** ± 3.28	-44.33** ± 1.87	-67.81** ± 13.67	-51.08** ± 13.63	-7.58** ± 2.05	32.51** ± 15.25	Duplicate
100 seed weight							
BCW 56 / C 20 R	2.26** ± 0.03	0.03 ± 0.02	-0.02 ± 0.11	0.06 ± 0.11	-0.04 ± 0.03	0.06 ± 0.13	Duplicate
BCW 56 / 1005	1.90** ± 0.03	0.45** ± 0.04	0.59** ± 0.14	0.40** ± 0.13	-0.06 ± 0.05	-0.50** ± 0.21	Duplicate
C 20 R / DR 714-1-2R	--	--	--	--	--	--	--
C 20 R / 1005	1.73** ± 0.02	0.59** ± 0.03	1.18** ± 0.11	0.88** ± 0.11	0.13** ± 0.03	-0.74** ± 0.14	Duplicate
DR 714-1-2R / 1005	1.88** ± 0.02	0.38** ± 0.04	0.16 ± 0.12	0 ± 0.12	-0.01 ± 0.04	-0.15 ± 0.17	Duplicate
Kernel length							
BCW 56 / C 20 R	6.16** ± 0.05	0.36** ± 0.05	-0.01 ± 0.23	-0.12 ± 0.22	-0.18** ± 0.07	-0.01 ± 0.31	Complementary
BCW 56 / 1005	6.30** ± 0.05	0.23** ± 0.05	-0.15 ± 0.22	-0.34 ± 0.21	-0.15* ± 0.07	0.63* ± 0.29	Duplicate
C 20 R / DR 714-1-2R	6.15** ± 0.04	-0.78** ± 0.06	0.43* ± 0.21	0.53** ± 0.20	0 ± 0.08	-0.71* ± 0.32	Duplicate
C 20 R / 1005	5.64** ± 0.03	-0.30** ± 0.03	0.97** ± 0.14	0.52** ± 0.13	-0.14** ± 0.04	-0.08 ± 0.18	Duplicate
DR 714-1-2R / 1005	6.28** ± 0.05	0.77** ± 0.03	0.86** ± 0.21	0.92** ± 0.19	0.15* ± 0.05	-1.30** ± 0.26	Duplicate
Kernel breadth							
BCW 56 / C 20 R	2.46** ± 0.02	-0.16** ± 0.02	-0.03 ± 0.09	0.19* ± 0.09	0.00 ± 0.03	0.32* ± 0.13	Duplicate
BCW 56 / 1005	2.16** ± 0.02	0.11** ± 0.02	0.03 ± 0.08	-0.11 ± 0.07	-0.06* ± 0.03	-0.04 ± 0.12	Duplicate
C 20 R / DR 714-1-2R	2.43** ± 0.01	0.21** ± 0.02	-0.44** ± 0.08	0.47** ± 0.07	-0.01 ± 0.03	0.54** ± 0.13	Duplicate
C 20 R / 1005	--	--	--	--	--	--	--
DR 714-1-2R / 1005	2.14** ± 0.02	0.07** ± 0.01	-0.33** ± 0.09	-0.41** ± 0.08	-0.03 ± 0.02	0.34** ± 0.11	Duplicate
Kernel l/b ratio							
BCW 56 / C 20 R	2.52** ± 0.03	0.32** ± 0.04	0.04 ± 0.15	0.14 ± 0.14	-0.07 ± 0.05	-0.31 ± 0.20	Duplicate
BCW 56 / 1005	--	--	--	--	--	--	--
C 20 R / DR 714-1-2R	2.54** ± 0.03	-0.60** ± 0.05	0.69** ± 0.16	0.82** ± 0.15	0 ± 0.06	-0.96** ± 0.26	Duplicate
C 20 R / 1005	2.46** ± 0.03	-0.43** ± 0.02	0.07 ± 0.14	0.16 ± 0.13	0.03 ± 0.04	0.23 ± 0.18	Complementary
DR 714-1-2R / 1005	2.94** ± 0.04	0.26** ± 0.02	0.87** ± 0.17	1.01** ± 0.16	0.12** ± 0.05	-1.08** ± 0.22	Duplicate
Grain yield per plant							
BCW 56 / C 20 R	8.55** ± 0.57	-0.61 ± 0.53	24.70** ± 2.63	19.10** ± 2.51	-0.51 ± 0.65	-8.10* ± 3.48	Duplicate
BCW 56 / 1005	7.46** ± 0.61	-2.27** ± 0.85	54.37** ± 3.43	37.69** ± 2.99	-2.02* ± 0.95	-18.15** ± 5.37	Duplicate
C 20 R / DR 714-1-2R	16.24** ± 0.57	-0.44 ± 0.64	17.42** ± 2.99	2.51 ± 2.96	-0.66 ± 0.70	12.43** ± 3.77	Complementary
C 20 R / 1005	16.01** ± 1.04	-0.25 ± 0.62	10.18* ± 4.39	0.88 ± 4.35	-0.09 ± 0.74	6.86 ± 4.97	Complementary
DR 714-1-2R / 1005	13.98** ± 0.73	-4.37** ± 0.53	11.43** ± 3.14	5.19 ± 3.11	-4.00** ± 0.64	-0.64 ± 3.74	Duplicate

* and ** indicate significance of values at P=0.05 and 0.01, respectively

and hence, this cross can be utilized for heterosis breeding. Three crosses exhibited duplicate epistasis for this character. The important contribution of dominance effect and duplicate gene action for this character was also explained by Dhanakodi and Subramaniam (1994) and Hasib *et al.* (2002).

The crosses BCW 56 / C 20 R and BCW 56 / 1005 recorded significant 'h' and 'i' epistatic components for inheritance of panicle length. The 'h' component is higher in magnitude than 'i' component. Biparental mating and reciprocal recurrent selection can be utilized for exploiting dominance and additive x additive type of epistasis. This type of inheritance for panicle length was also reported by Ram (1994); Hasib *et al.* (2002) and Verma *et al.* (2006). Since in cross BCW 56 / C 20 R 'd' and 'i' components are significant, selection can be done in the early generations by spotting true breeding genotypes for panicle length. Four crosses exhibited duplicate type of epistasis for this character.

Number of filled grains per panicle exhibited highly significant 'd' 'h' and 'i' type epistatic gene actions in crosses BCW 56 / C 20 R, BCW 56 / 1005 and C 20 R / DR 714-1-2R. Since 'h' effects arising from non additive gene action cannot be fixed in nature, heterosis breeding can be exploited in the above crosses by crossing the parents as male with high yielding CMS sources for identifying heterotic combinations. Though, dominance 'h' component was highly significant, the additive x additive 'i' epistatic inheritance is equally significant. Therefore, alternately, careful selections could also be rewarding to get homozygous lines for this character from segregating generations. All the crosses exhibited duplicate type of epistasis for this character which was also observed by Banumathy and Thiyagarajan (2005) and Murugan and Ganesan (2006).

The character 100 seed weight was governed by both additive 'd' and dominance 'h' with highly significant 'i' epistatic interaction component in BCW 56 / 1005 and C 20 R / 1005. Therefore, reciprocal recurrent selection and biparental mating in early segregating generation followed by selection would be more rewarding in these crosses to increase 100 seed weight. All the crosses exhibited duplicate type of gene action. Similar results stating the predominant role of dominance and epistasis for this trait was also reported by Verma *et al.* (2006).

The dominance 'h' effect was more prominent than

additive 'd' gene effect in the inheritance of grain yield which is ascertained by the non-significant nature of additive genetic variance in most of the crosses. The crosses BCW 56 / C 20 R and BCW 56 / 1005 recorded significant 'h' and 'i' type of epistasis. Preponderance of dominance and additive x additive type suggests that one can expect to select better lines in segregation generations after restoring to biparental mating followed by selection. The greater importance of dominance gene effect than the additivity for grain yield per plant was also reported by Singh *et al.* (2009). The crosses C20 R / DR 714-1-2R, C 20 R / 1005 and DR 714-1-2R / 1005 exhibited significant 'h' variance while, cross C20 R / DR 714-1-2R is governed additionally by significant dominance x dominance (l) gene action besides dominance. The signs of 'h' and 'l' were positive and are in the same direction for cross C20 R / DR 714-1-2R and C 20 R / 1005 which signifies complementary type of digenic non allelic interaction. Since these crosses were selected based on highest heterosis and heterobeltiosis for grain yield per plant and due to presence of dominance and dominance x dominance gene effect with complementary digenic inter allelic interaction, the parents of these crosses *i.e.*, C 20 R, DR 714-1-2R and 1005 could be used as male parents against the CMS lines for development of heterotic hybrids for grain yield.

For the character kernel length, the crosses BCW 56/C 20 R, BCW 56/1005 and DR 714-1-2R/1005 exhibited significant additive gene effects (*i*) whereas, three crosses *viz.*, 20 R / DR 714-1-2R, C 20 R/1005 and DR 714-1-2R / 1005 exhibited dominance (*h*). Selection for isolating desirable lines with good kernel length in the crosses exhibiting additive gene action will be desirable, while heterotic breeding will be rewarding to exploit non additive gene action in the crosses exhibiting dominance variance or else selection can be postponed to later generations when dominance is dissipated for isolating homozygous lines. The cross DR 714-1-2R / 1005 exhibited significant effects for 'd' 'h' 'i' and 'j' components. Therefore, biparental mating followed by selections in the early generations will be useful for isolating purelines of restorers for this character. Four crosses exhibited duplicate epistasis.

Additivity is governing kernel breadth in crosses BCW 56/1005 ($d=0.11^{**}$), C 20 R/DR 714-1-2R($d=0.21^{**}$, $i=0.47^{**}$) and DR 714-1-2R / 1005($i=0.07^{**}$) in whose case simple pedigree selection helps in

improving this character. The cross C20 R / DR 714-1-2R exhibited significant additive variance with significant dominance x dominance variance and hence reciprocal recurrent selection and biparental mating in early segregating generation followed by selection would be more rewarding in this cross where additive and non additive gene actions could be exploited simultaneously. All the crosses exhibited duplicate type of epistasis.

Kernel length/breadth ratio was governed by all types of gene effects viz., 'd' 'h' 'i' and 'j' epistasis effects in cross DR 714-1-2R/1005. Therefore, population improvement programme followed by selection is desirable. The cross C20 R / DR 714-1-2R exhibited significant dominance and additive x additive epistasis. Hence, homozygous lines for this character can be isolated from this cross by switching to biparental mating followed by selection. In BCW 56 / C 20 R ($d = 0.32^{**}$) and C 20 R / 1005 ($d = -0.43^{**}$) this trait is under additive gene action and thus simple pedigree selection could help in isolating desirable types from segregating generations. Three crosses exhibited significant duplicate type of epistasis. Similar gene effects were also reported for kernel length and kernel L/B ratio by Hasib *et al.* (2002).

Conclusion:

From the ongoing discussion on gene action in quantitative traits of rice, additive (d) and additive x additive (i) gene effects were the only significant components for the inheritance of the trait days to 50 per cent flowering in cross BCW 56 / C 20 R, BCW 56 / 1005 and C 20 R / DR 714 -1- 2R. Additive (d) gene effects alone are highly significant for the expression of 100 seed weight in cross DR 714-1-2R / 1005, kernel l/b ratio in crosses BCW 56 / C 20 R and C 20 R / 1005. These additive (d) and additive x additive (i) gene effects are fixable and are most easily exploited by producing

homozygous genotypes. Hence, these traits in the above respective crosses offer scope for restorer line improvement through phenotypic selection based on pedigree method and simple selection in the segregating generations. Further, the study revealed non-additive component of epistasis was more important than the additive gene action in the inheritance of most of the yield and quality characters like plant height, number of panicles plant⁻¹, panicle length, number of filled grains panicle⁻¹, 100 seed weight, grain yield plant⁻¹, kernel length, kernel breadth and kernel L/B ratio in most of the crosses studied. Predominance of duplicate type of epistasis as evidenced from opposite sign of (h) and (l) was also noticed in majority of crosses which depicts non allelic interaction. This type of epistasis tends to cancel or weaken the effects of each other and hinders the progress made under selection. Therefore, selection would have to be deferred till later segregating generations where dominance effects are dissipated. Population improvement concept may become an amenable solution in autogamous crops like rice (Frey, 1975). Biparental mating, reciprocal recurrent selection and diallele selective mating systems (Jenson, 1970) might be profitable in breaking the gene linkages and exploiting both additive and non additive gene actions to obtain desirable recombinants having the characteristics of a restorer line like tall plants, desirable flowering duration to match with CMS parent in hybrid combination, reduced flag leaf area for better pollen dispersal and more number of fertile spikelets and grain yield.

The conclusion drawn from the gene effects for different characters are based on digenic interaction model assuming two genes in the character inheritance. However, possibilities of trigenic or higher order interactions and linkages among the genes governing cannot be ruled out.

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